Ornis Fennica 88:14–29. 2011

Persistence of Capercaillie (*Tetrao urogallus*) lekking areas depends on forest cover and fine-grain fragmentation of boreal forest landscapes

Saija Sirkiä, Pekka Helle, Harto Lindén, Ari Nikula, Kai Norrdahl, Petri Suorsa & Pentti Valkeajärvi

S. Sirkiä, Department of Biosciences, Viikinkaari 1, P.O. Box 65, FI-00014 University of Helsinki, Finland; Finnish Game and Fisheries Research Institute, P.O. Box 2, FI-00791 Helsinki, Finland. E-mail saija.sirkia@helsinki.fi
P. Helle, Finnish Game and Fisheries Research Institute, Tutkijantie 2 E, FI-90590 Oulu, Finland. E-mail pekka.helle@rktl.fi
H. Lindén, Finnish Game and Fisheries Research Institute, P.O. Box 2, FI-00791 Helsinki, Finland. E-mail harto.linden@rktl.fi
A. Nikula, Finnish Forest Research Institute, Rovaniemi Research Unit, P.O. Box 16, FI-96301 Rovaniemi, Finland. E-mail ari.nikula@metla.fi
K. Norrdahl, Department of Biology, Section of Ecology, University of Turku, FI-20014 Turku, Finland. E-mail kai.norrdahl@utu.fi
P. Suorsa, Talolankatu 5 B 14, FI-20460 Turku, Finland. E-mail petri.suorsa@utu.fi
P. Valkeajärvi, Finnish Game and Fisheries Research Institute, Survontie 9, FI-40500 Jyväskylä, Finland. E-mail pentti.valkeajarvi@rktl.fi

Received 7 May 2010, accepted 17 August 2010

We studied the effects of habitat loss, fragmentation and their interaction on the persistence of Capercaillie lekking areas at three study areas in Finland. We inspected a total of 381 leks twice with an interval of 10–30 years, and classified them as persisting versus ceased leks. We attempted to explain the persistence of Capercaillie leks with forest cover and fine-grain fragmentation at two spatial scales (within 1,000 m and 3,000 m from the leks) by using satellite-image based forest-inventory data. We statistically removed the effect of forest cover from the measure of fragmentation, and used information-theoretical model selection to evaluate a set of logistic regression analyses. Fine-grain forest fragmentation had a positive effect on lek persistence. Forest cover positively affected lek persistence only when considering the landscapes surrounding the leks (within 3,000 m radius). In addition, we found a significant negative interaction between forest cover and fragmentation. Under conditions of low forest cover, patch configuration may become increasingly important for the persistence of lekking areas. According to our results, the most effective management strategies for Capercaillie lekking areas include maximizing the amount of forest around the lekking areas, and encouraging mosaic-like variability of the forest.

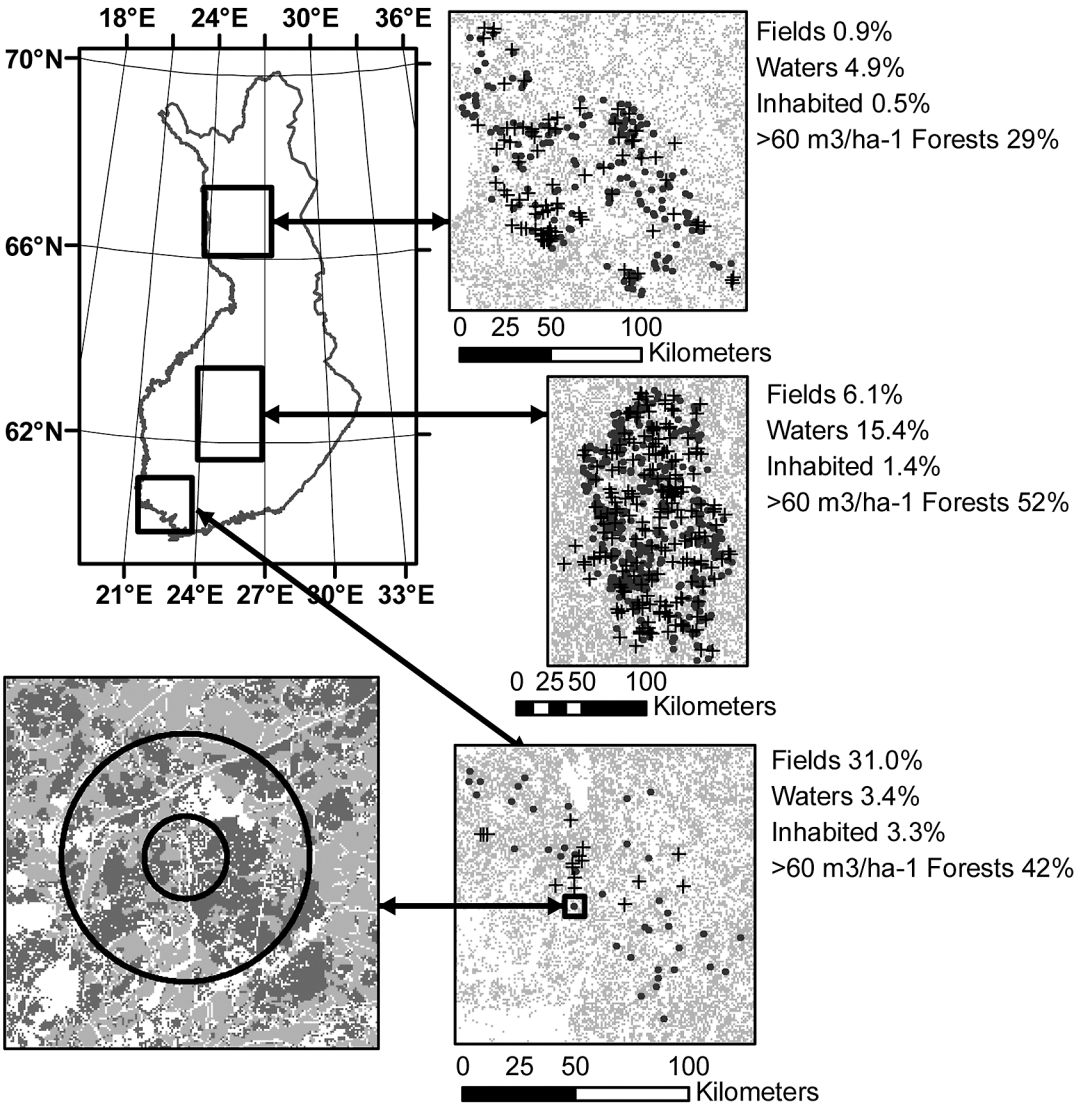

Fig. 1. The study areas: South-western, Central and Northern Finland. Dots and crosses represent persisting and ceased leks, respectively. The proportions of fields, waters and inhabited areas in the landscape describe the differences in the matrices between the study areas, whereas the proportion of forests (> 60 m^3 ha^{-1}) shows the amount of habitat for each area. The two spatial scales (1,000 and 3,000 m radii around the centre of each lek) are shown for an example lekking site.

1. Introduction

In spring, Capercaillie (*Tetrao urogallus*) males collect to display at traditional lekking sites (i.e., displaying arenas). Females visit these sites during a relatively short period to copulate, but males stay in the surrounding areas of leks year round (e.g., Wegge & Larsen 1987). The minimum size for a lekking area is 300 hectares and includes the lekking site plus the surrounding daily territories of the males, i.e., the area for the lekking males to rest and feed between the actual displaying and mating (Wegge & Larsen 1987). As a consequence, landscape-level processes are thought to affect the ecology of the species (Sjöberg 1996). According to Rolstad & Wegge (1987a), the number of Capercaillie males per lek is positively correlated with fine-grain fragmentation of forest at

Table 1. Habitat classes and structural variables of forests within r = 3,000 m surrounding persisting and ceased Capercaillie leks at three study areas in Finland (see Fig. 1). Values correspond to the percentage of habitat cover in 25 m × 25 m pixels. In the habitat classes marked with a cross (†), the criterion for tree-species composition is ≥ 80% of total volume (of forests > 60 m^3 ha^{-1} on mineral soil). The criterion for bogs covers forests ≥ 10 m^3 ha^{-1} growing on peatland, whereas that for sapling stands covers forests 10–60 m^3 ha^{-1} on mineral soil. Treeless bogs and clear-cuts cover forests < 10 m^3 ha^{-1} on both soil types. Both soil types are combined in the structural variables. Variables marked with a star (*) are calculated for the forest (> 60 m^3 ha^{-1}) versus open land. IQR = inter-quartile range, PD = patch density, MPS = mean patch size, ED = edge density and MNN = mean nearest-neighbour distance.

Habitat class, %	SW Finland (*N*=55)		CE Finland (*N*=238)		NO Finland (*N*=88)	
	Range	Median (IQR)	Range	Median (IQR)	Range	Median (IQR)
Open habitats	11.0–66.4	28.2(15.1)	8.0–75.8	24.8(17.4)	5.8–39.8	18.5(12.3)
Bogs	2.5–28.0	9.8(11.2)	0.1–47.8	12.4(16.3)	10.4–61.7	31.7(19.7)
Pine forest†	0.3–26.3	5.0(2.8)	0.6–26.9	7.4(8.0)	1.8–31.7	9.3(8.4)
Spruce forest†	0.2–6.4	1.0(0.9)	0.1–11.1	1.6(2.5)	0.0–0.4	0.02(0.1)
Deciduous forest†	0.0–1.3	0.2(0.2)	0.1–5.0	0.6(0.9)	0.0–0.3	0.001(0.0)
Mixed forest	17.4–61.6	43.8(9.1)	16.3–53.2	33.6(11.3)	2.4–36.9	12.0(7.4)
Sapling stands	4.3–18.0	8.4(4.2)	3.5–19.6	11.4(4.2)	8.7–47.2	23.3(10.1)
'Open habitats' class,%						
Lakes	0.0–15.8	0.6(2.1)	0.1–69.9	7.0(12.4)	0.0–20.6	1.6(4.8)
Agricultural fields	2.9–57.9	16.1(18.7)	0.0–24.4	4.8(5.5)	0.0–5.0	0.02(0.3)
Human settlements	0.2–8.8	1.2(1.2)	0.0–13.4	0.4(0.5)	0.0–2.1	0.04(0.1)
Roads	1.9–6.4	3.6(1.2)	1.4–5.8	3.5(1.2)	0.0–2.2	1.0(0.6)
Treeless bogs and clear-cuts	0.1–12.9	1.5(2.6)	1.3–23.4	6.5(3.6)	2.9–33.7	11.8(9.9)
Forest structural variables						
Cover (> 60 m^3ha^{-1})	26.8–75.9	59.1(16.5)	20.7–77.0	57.9(13.4)	8.4–60.3	29.6(4.6)
PD (# per 100 ha)*	1.8–13.1	5.5(2.9)	2.6–12.6	6.2(2.9)	7.8–44.4	23.4(8.9)
MPS (ha)*	3.4–37.8	10.2(8.9)	2.7–24.3	9.1(5.9)	0.3–6.7	1.2(1.0)
ED (m ha^{-1})*	73.7–162.0	115.2(26.7)	49.5–169.3	128.1(21.7)	69.7–220.0	140.2(40.1)
MNN (m)*	29.3–63.1	35.6(7.2)	26.9–65.6	32.0(4.8)	29.1–48.1	34.2(4.6)

the leks surrounded by 50–60% of old (> 60–70 years) forest. In addition, the number of displaying males is positively correlated with the persistence of lekking sites (Rolstad & Wegge 1989a).

The aim of the present study was to examine the effects of habitat loss and fragmentation on the persistence of Capercaillie lekking areas (as defined above; Wegge & Larsen 1987) at three study areas in Finland, representing different degrees of human influence. Habitat loss affects the distribution and movement of animals, and increases the isolation and extinction risk of local populations (With & Crist 1995, Harrison & Bruna 1999). Habitat preservation should therefore be a priority in species conservation (e.g., Fahrig 1999, 2001). Habitat fragmentation, on the other hand, may have both positive and negative effects on biodiversity (Fahrig 1997, 1999, 2003, Jokimäki *et al.* 2000, Cooper & Walters 2002). Effects of fragmentation depend on, for example, the response of an organism to environmental heterogeneity (e.g., fine- or coarse-grain response; Addicott *et al.* 1987, Rolstad & Wegge 1987a, 1989b). Fine-grain, mosaic-like responses to fragmentation often have positive effects mainly because a landscape that consists of many habitat patches can more easily satisfy the habitat requirements of a given species (Forman & Godron 1986, Helle *et al.* 1994). For example, in southern Finnish silvicultural mosaics, high habitat heterogeneity increased the abundance of forest birds (Raivio & Haila 1990). Since species' responses can also depend on the extent of fragmentation in relation to different spatial and temporal scales (Wiens 1989, Levin 1992, Fuhlendorf *et al.* 2002, Keppie & Kierstead 2003), we studied these landscape phe-

Table 2. The lekking-area data-collection years and sample sizes for the three study areas (see Fig. 1). General abundance is the average number of Capercaillie per km^2 of forest in the corresponding game management district over 1990–2009 (data from the wildlife triangle scheme; Lindén *et al*. 1996). SW = South-western, CE = Central and NO = Northern Finland.

	SW	CE	NO	Total
General abundance	1.96	3.33	3.55	
Old survey	1970–80	1972–73	1987–92	
New survey	2000–2005	1990–2005	2000–2005	
Persisting leks (*N*)	39	37	69	145
Ceased leks (*N*)	16	201	19	236
Total *N* (% ceased)	55 (29)	238 (84)	88 (22)	381 (62)

nomena at two spatial scales, viz. 1,000 m and 3,000 m radii.

We were especially interested in examining possible interactions between these effects, i.e., to see if the effect of habitat fragmentation increases with decreasing habitat cover, or vice versa. The effects of habitat configuration (i.e., fragmentation per se) may become apparent only when the amount of suitable habitat has decreased to 10–30% of the landscape (Andrén 1994, Fahrig 1997, 1998, Betts *et al.* 2006). Although it is important to distinguish between the effects of habitat loss and fragmentation (McGarigal & Cushman 2002), it is in practice difficult because these two processes occur simultaneously in nature (Fahrig 1997, 1999, Villard *et al.* 1999). Statistically however, it is possible to remove the effect of forest cover from the indices of fragmentation, and to create an independent measure for habitat fragmentation (see Trzcinski *et al.* 1999).

Finally, we aimed to incorporate knowledge about the interaction between landscape-scale habitat cover and fragmentation into the conservation and management of Capercaillie lekking areas. In general, habitat loss, habitat degradation and coarse-grain fragmentation are major threats to several species groups worldwide (Hannah *et al.* 1995, Esseen *et al.* 1997, Mönkkönen 1999), including tetraonids (Storch 2000, 2007). The yearly grouse censuses have documented rapid declines of Capercaillie populations throughout Finland during the past 50 years (e.g., Lindén & Rajala 1981, Helle *et al.* 2003). These declines have, however, partly stabilized from the 1990s onwards (Lindén 2002). Conservation of the lekking areas of the Capercaillie might be beneficial also for other forest-dwelling birds, because the overall richness of breeding forest birds appears higher in the vicinity of Capercaillie leks, compared to "average" forest (Pakkala *et al.* 2003).

2. Material and methods

2.1. Study areas and the lekking-area occupancy data

We conducted the research at three areas situated in (1) South-western (SW), (2) Central (CE), and (3) Northern Finland (NO; Fig. 1). In all areas, forests surrounding the lekking areas are dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.), with birches (*Betula* spp.), with other deciduous trees also present (Table 1). In NO Finland the matrix (here, non-forest area surrounding the lekking areas) consists mainly of open bogs and areas clear-cut for regeneration. In SW and CE Finland the matrix consists mainly of agricultural fields and waterbeds, respectively (Table 1). These three areas provide different habitat and matrix types across the south-north axis of Finland, also depicting the decreasing overall productivity towards the north, and a different degree of human impact (Fig. 1).

The lekking-area occupancy data were first collected in 1970–1992 (hereafter referred to as "old survey"), and the same sites were resurveyed mostly in 2000–2005 ("new survey"; Table 2). In NO Finland there was a period of about 10 years between the surveys, whereas in SW and CE Finland the period was 20–30 years. The data were mainly collected by Metsähallitus (Finnish Forest and Park Service; in NO Finland), by Finnish Game and Fisheries Research Institute (in CE Fin-

land; especially P. Valkeajärvi and his team) and by questionnaires and interviews from local game districts, land owners and hunters (in SW Finland). The sites were visited one or more times during the lekking season in March–May, and seen/heard Capercaillie individuals, snow tracks or fresh excrement were all interpreted as indicating an occupied lekking area. We spatially referenced the lekking sites to a digital map, and classified the occupancy data according to the distance between leks of the old and new survey. If the leks in the old and new survey were ≤ 1,000 m apart, we classified these sites as persisting leks (i.e., the centre of the lek had moved inside the radius of 1,000 m from year to year but the lekking area had presumably remained the same; Rolstad & Wegge 1989a, c), whereas we classified sites with old leks > 1,000 m away from new leks as ceased leks. Because the new survey was more intensive than the old one, the remaining group of leks (new leks > 1,000 m away from the old ones) could contain leks that were already in use in 1970–1992 but were missed by the surveyors. Hence, we did not include this category of leks in statistical analyses. We chose the central point of a given, persisting lek according to the new survey in case it had moved (see section 2.3).

2.2. Landscape data

We derived the land-use and forest-resource data from multi-source national forest inventory (MS–NFI) data (Tomppo *et al*. 2008). In Finland, the MS–NFI exploits Landsat TM 5 satellite images and ground reference plots in order to obtain geographically explicit information of forest resources. Digital maps of roads, agricultural land, and other non-forest land are used to separate non-forest from forest land (Katila & Tomppo 2002). MS–NFI uses the *k*-nearest-neighbours (*k*-nn) method in calculating forest parameters for each pixel that correspond to 25 m × 25 m land area. The result is a rectified multi-channel image that gives estimates of, e.g., stand age and growing-stock volume of all main tree species (pine, spruce, birch, and other deciduous trees as a combined class; Tomppo *et al*. 2008). The satellite images from SW, CE and NO Finland originate from 1998, 1996 and 2002–2003, respectively.

Having imported the NFI database and digital maps of non-forest areas into GIS, we reclassified each pixel by combining information of separate forest variables for every pixel. At a single-pixel level and up to 30–50 ha, satellite-image-based forest inventory is not accurate for detailed forest-structure parameters (Tokola & Heikkilä 1997). Depending on tree-species composition, the estimates of growing stock can have relative error of several tens of per cent, but decrease to some 10–20% for larger areas (Tokola & Heikkilä 1997). Therefore, and because the focus of the present study was in habitat loss and fine-grain fragmentation effects, we classified the landscape data simply as habitat and matrix. The former included all forest pixels having volume of timber above a threshold criterion of 60 m^3 ha^{-1} (see below) while all the other areas, such as roads, inhabited areas, fields, water and forests below the criterion were classified as matrix. Here, a forest patch is therefore always represented by either a single forest pixel (25 m × 25 m) or a group of adjacent forest pixels separated from other similar pixel groups (forest patches) with an at least 25-m wide belt of matrix pixels.

Although Capercaillie has traditionally been considered a specialist of old forests (Rolstad & Wegge 1987b, Helle *et al.* 1989), the species also seems to tolerate or even benefit from mosaic-like forests with varying tree-species composition and stand structure (Winqvist 1983, Helle *et al.* 1994), younger forest classes (e.g., thinned forests with dominant trees 30–90 years old; Miettinen *et al.* 2005), and moderate forestry operations (Rolstad & Wegge 1989c). Therefore, we defined habitat to include all pixels with > 60 m^3 ha^{-1} of timber, which refers to all the successional stages from young, thinned stands to forests > 61 years in NO Finland and forests > 41 years in CE and SW Finland (diameter at 1.3 m height ≥ 8 cm; Peltola 2003).

2.3. Landscape predictors

We calculated several indices to describe landscape structure surrounding Capercaillie leks for two spatial scales using FRAGSTATS (McGarigal & Marks 1995). First, we chose a spatial scale covering the whole lekking area, i.e. a circle with a ra-

Table 3. Pearson correlation coefficients indicating correlations between three indices representing forest fragmentation (MPS = mean patch size; PD = patch density; TE = total edge) and cover of forest (> 60 m^3 ha^{-1}). Coefficients for r = 1,000 m and r = 3,000 m are shown in the upper right and lower left corners of the table, respectively. All relationships were significant at $P \leq 0.0008$ except for the relationship between total edge and cover on 1,000 m scale, which was non-significant ($P > 0.05$).

Index	MPS	PD	TE	Cover
MPS		–0.46	–0.31	0.54
PD	–0.74		0.25	–0.83
TE	–0.17	0.32		–0.01
Cover	0.80	–0.76	0.17	

Table 4. Principal component loadings for the indices representing forest fragmentation (compare Table 3).

Radius (m)	Index	PC1	PC2
1,000	Mean patch size	–0.63	0.24
	Patch density	0.60	–0.46
	Total edge	0.50	0.86
	% of variation explained	56	26
3,000	Mean patch size	–0.64	0.37
	Patch density	0.67	–0.15
	Total edge	0.37	0.92
	% of variation explained	63	29

dius of 1,000 m around the central point of a lek, covering 314 ha. This area roughly covers the daily territories of the males, i.e., the area required by lekking males to rest and feed between the actual displaying events (Wegge & Rolstad 1986, Wegge & Larsen 1987, Storch 1997, Wegge *et al.* 2003). At this scale, parameters of forest structure derived from satellite images are also reliable enough for analyzing forest structure. In an earlier study concerning habitat use of Capercaillie in the Swiss Alps, the scale of r = 900 m (253 ha) performed best for single-scale models (Graf *et al.* 2005).

The second spatial scale, a circle with a radius of 3,000 m, represents the landscape context in which the lekking areas were embedded, thus covering 2827 ha. When examining the effects of habitat loss and fragmentation, it is important to use large spatial scales and whole landscapes instead of single forest patches (Forman & Godron 1986, Fahrig 2003). We acknowledge that the use of this larger spatial scale introduces some spatial overlapping in the landscape analysis. Particularly in heavily-fragmented landscapes, where forested areas are embedded in a matrix consisting mostly on agricultural land and human settlements, areas adjacent to lekking sites up to a few kilometres from the lek centre may be of importance to Capercaillie (Helle *et al.* 1994). Hence, we assume that the persistence of the lekking areas of Capercaillie depends at least partly on different habitat-selection processes at different spatial scales (see also Storch 2002, Graf *et al.* 2005).

We calculated the landscape structure separately for both radii and selected the following indices for modelling: forest cover (proportion of forest cover within the total area); mean patch size (MPS; ha); patch density (PD; number of patches per 100 ha) and total edge between patches of forest and non-forest (TE; m) ('Forest structural variables' in Table 1). Forest cover (> 60 m^3 ha^{-1}) refers directly to the amount of focal habitat in the landscape, whereas MPS, PD and TE refer to the spatial arrangement of forest patches, and hence define the degree of fine-grain fragmentation in the landscape (Trzcinski *et al.* 1999). Because of the fairly small pixel size (25 × 25 m) in our analysis, we assume that fragmentation is experienced mostly as forest heterogeneity or mosaic structure and acts mainly at the level of individual birds (e.g., food and cover associated with diverse habitat types). This contrasts with coarse-grain responses to fragmentation, which are thought to act mainly by limitating population-level resource use, movements or dispersal (see Addicott *et al.* 1987, Haila 1990, Niemuth & Boyce 2004).

2.4. Fine-grain fragmentation index

We used a correlation-based Principal Component Analysis (Proc PRINCOMP, SAS 8.2; Isebrands & Crow 1975) for both spatial scales separately to obtain fragmentation indices from MPS, PD and TE (hereafter referred to as indices for "effects of fragmentation"). The indices were strongly corre-

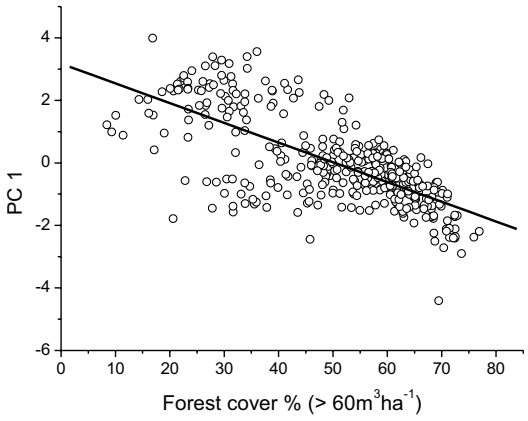

Fig. 2 The first principal component (PC1) representing fine-grain forest fragmentation and percentage of forest cover (> 60 m^3ha^{-1}) at the 3,000-m spatial scale (N = 381, r = –0.70, P < 0.0001). The graph for the 1,000-m spatial scale looked essentially the same and is therefore not shown.

lated with each other (Table 3). Over 80% and 90% of variation was explained by the first two components on 1,000 m and 3,000 m spatial scales, respectively. At both spatial scales, we defined the first principal component (PC1) as being a measure of fine-grain forest fragmentation (FRAG) because PC1 embodied the three simultaneous effects of fragmentation (Trzcinski *et al.* 1999). As PC1 increased, mean forest-patch size decreased, patch density of forest patches increased and the amount of forest/non-forest edge increased (Table 4). We removed the correlation between PC1 and forest cover by using linear regression (Fig. 2), and used the residuals as a measure of forest fragmentation that is independent of forest cover.

2.5. Statistical models

To analyze the data, we used logistic regression models (GENMOD procedure, SAS 8.2) where lek (persisting versus ceased; binomial distribution, logit link function) was treated as a dependent variable. The models first included all lekking areas (N = 381). Because the 3,000-m spatial scale includes information of the smaller radius, the modelling was conducted separately for the two spatial scales (1,000 and 3,000 m).

To examine the potential effects of fine-grain forest fragmentation, forest cover and their interaction on lek persistence, we selected four competing models following mainly the hypotheses reviewed by Betts *et al.* (2006). The first model represented the null hypothesis which states that lek persistence is only affected by the initial sample collected in different study areas (the class variable LOCAT, derived from "location"). The second model followed the landscape fragmentation hypothesis (Villard *et al.* 1999) with forest fragmentation (FRAG) as the main factor affecting the lek persistence. The third model tested the landscape composition hypothesis in which the amount of forest habitat (COVER) at the landscape level is considered the single most important predictor (Fahrig 2003). In the fourth model we followed the non-linear fragmentation hypothesis (Andrén 1994, Fahrig 1997, 1998, Betts *et al.* 2006) which postulates that landscape configuration only becomes important after some critical threshold in habitat amount is passed (significant interaction FRAG*COVER). Because of the obvious differences between the study areas (Table 1), we included the variable describing study area (LOCAT) and all relevant interaction terms with study area (FRAG*LOCAT, COVER*LOCAT and FRAG*COVER*LOCAT) simultaneously into the models as explanatory variables. For those variables that had a significant ($P \leq 0.05$) interaction with the term LOCAT, we ran new models for the separate study areas. Preliminary analyses suggested that the period between the lekking-area surveys at different study areas was redundant.

We conducted model selection by using Akaike's Information Criteria (AIC; Burnham & Anderson 1998). We interpreted the difference between the best model and candidate models (Δ_i) as follows: (1) if $D_i < 2.0$, the difference is non-significant; (2) if $2.0 < D_i < 7.0$, the difference is significant; or (3) if $D_i > 7.0$, the difference is highly significant. We used Akaike weight (w_i) to indicate the degree of belief that the model is the best when considering the data and other candidate models.

3. Results

3.1. Model selection

At the spatial scale of 1,000 m, the fourth model in which we tested the non-linear fragmentation hy-

Table 5. AIC scores for the candidate models explaining Capercaillie lek occupancy for (a) r = 1,000 m and (b) r = 3,000 m (N = 381 for both spatial scales).

a. Model	Model structure	df	np	dev	AIC	D_i	w_i
4	FRAG + COVER + LOCAT + FRAG*LOCAT + COVER*LOCAT + FRAG*COVER + FRAG*COVER*LOCAT	369	12	347.79	719.58	0	0.995
3	COVER + LOCAT + COVER*LOCAT	375	6	359.42	730.84	11.26	0.004
1	LOCAT	378	3	363.81	733.61	14.03	0.001
2	FRAG + LOCAT + FRAG*LOCAT	375	6	362.45	736.90	17.32	0.000

b. Model	Model structure	df	np	dev	AIC	D_i	w_i
3	COVER + LOCAT + COVER*LOCAT	375	6	356.33	724.65	0	0.808
4	FRAG + COVER + LOCAT + FRAG*LOCAT + COVER*LOCAT + FRAG*COVER + FRAG*COVER*LOCAT	369	12	351.82	727.64	2.98	0.182
1	LOCAT	378	3	363.81	733.61	8.96	0.009
2	FRAG + LOCAT + FRAG*LOCAT	375	6	362.66	737.33	12.67	0.001

pothesis (Andrén 1994, Fahrig 1997, 1998, Betts *et al.* 2006) appeared the best among the set of candidate models (Table 5a). The difference to the second-best model was highly significant (D_i > 11.0). In contrast, at the spatial scale of 3,000 m, the model that tested the landscape composition hypothesis (COVER; Fahrig 2003) performed best among the candidate models (Table 5b). The difference to the second-best model was significant (D_i > 2.0), and Akaike weight supported the view that the model is the best when considering the data and other candidate models (w_i = 0.808).

Table 6. Logistic-regression-based likelihoods of the persistence of Capercaillie leks for r = 1000 m and r = 3000 m (N = 381). Model selection was performed by using AIC (see Table 5). FRAG = fine-grain fragmentation index, COVER = forest cover (proportion of forests > 60 m^3ha^{-1}), LOCAT (1) = SW Finland versus NO Finland, LOCAT (2) = CE Finland versus NO Finland (NO Finland was set as the reference).

Radius (m)	Variable	Estimate	SE	DF	χ^2	P
1,000	Intercept	0.718	0.842	1	0.73	0.394
	FRAG	0.375	0.461	1	6.30	0.012
	COVER	0.040	0.031	1	0.85	0.356
	LOCAT (1)	–0.135	3.414	2	4.66	0.098
	LOCAT (2)	–3.101	1.476			
	FRAG*LOCAT (1)	5.021	3.721	2	3.90	0.142
	FRAG*LOCAT (2)	1.674	1.698			
	COVER*LOCAT (1)	–0.035	0.055	2	0.76	0.685
	COVER*LOCAT (2)	–0.029	0.036			
	FRAG*COVER	–0.030	0.014	1	9.06	0.003
	FRAG*COVER*LOCAT (1)	–0.036	0.050	2	0.71	0.701
	FRAG*COVER*LOCAT (2)	0.001	0.028			
3,000	Intercept	1.195	0.778	1	2.36	0.124
	COVER	0.003	0.024	1	5.34	0.021
	LOCAT (1)	–4.485	2.026	2	13.70	0.001
	LOCAT (2)	–4.222	1.318			
	COVER*LOCAT (1)	0.070	0.041	2	3.14	0.208
	COVER*LOCAT (2)	0.021	0.030			

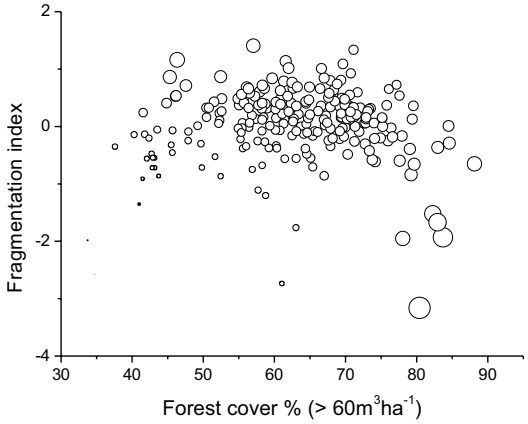

Fig. 3 Fine-grain forest fragmentation and forest cover and the persistence of leks in CE Finland at the 1,000-m spatial scale (χ^2 = 1.78, df = 1, P = 0.182). The data of predicted probability of lek persistence are indicated with symbol size, larger symbols indicating higher probability.

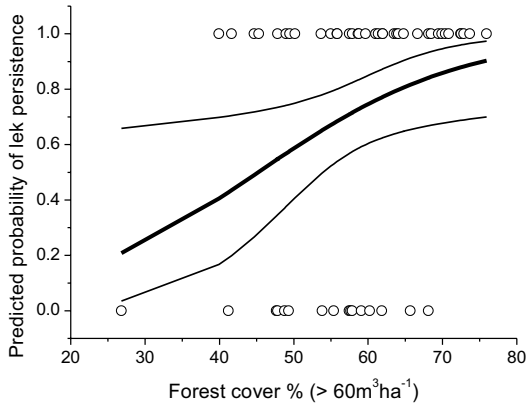

Fig. 4. Forest cover (> 60 m^3 ha^{-1}) and the probability of lek persistence in SW Finland at the 3,000-m spatial scale (χ^2 = 5.69, df = 1, P = 0.017). The graph shows 95% confidence limits along with a probability line, for which y = –3.29 + 0.073x (SE 0.033).

3.2. Effects of the landscape variables

At the 1,000-m spatial scale, fine-grain forest fragmentation (FRAG) had a significant positive effect on lek persistence, and also the interaction between forest fragmentation and cover (FRAG* COVER) appeared significant and negative (Table 6, Fig. 3). The interaction implies that the effect of fragmentation on the probability of lek persistence varied with different values of forest cover. More specifically, the highest probability of lek persistence was always achieved with high forest cover and low fragmentation, but with lower values for forest cover there was a small increase in the probability of lek persistence with higher fine-grain fragmentation (Fig. 3). In an example from CE Finland, this increase was around 50% forest cover (larger symbols in Fig. 3).

At the spatial scale of 3,000 m, forest cover had a significant and positive effect on lek persistence (Table 6, Fig. 4). Thus, there was a general tendency for the persisting lekking areas in Finland to be located within the largest forest patches. The term LOCAT did not significantly interact with the other model terms at either of the spatial scales, so separate modelling for study areas was not conducted.

4. Discussion

4.1. Effect of fine-grain fragmentation

In general, our measure of fragmentation could be interpreted as environmental heterogeneity that is needed for the species to fulfill its daily, seasonal and yearly activities (e.g., Leopold 1933, Niemuth & Boyce 2004). This heterogeneity may explain the positive effects of fine-grain fragmentation found in this study. Mosaic-like heterogeneity probably supports the growth of multi-layered forests which in turn provide food and cover for the individual birds, especially the males staying close to the lekking area year round (Helle *et al*. 1994). It is also noteworthy that if the amount of habitat is kept constant, increasing fragmentation per se actually implies shorter average distances between the separate forest patches (Fahrig 2003).

Fragmentation of very dense forest stands may also produce more space for Capercaillie males at the leks, particularly in SW and CE Finland. Although the Capercaillie is fairly flexible with respect to habitat characteristics of the lekking centre (Winqvist 1983), the density of trees should not prevent good visibility (Rolstad & Wegge 1987b), which should be around 20–50 m at the

height of 1 m (Valkeajärvi & Ijäs 1986). Dense, spruce-dominated undergrowth is rarely preferred by the Capercaillie, at least in Central Europe (Sachot *et al.* 2003, Thiel *et al.* 2007). In some Norwegian logging experiments, Capercaillie males have even preferred thinned forests when the forest at the original lekking site was too dense (Rolstad & Wegge 1989c, Rolstad *et al.* 2007). Especially in landscapes managed for forestry, fine-grain fragmentation may represent temporary, dynamic process where the border between suitable habitat patches and matrix may be hard to discriminate (Edenius & Elmberg 1996, Norton *et al.* 2000, Schmiegelow & Mönkkönen 2002). Capercaillie males might adapt to such dynamic forest environment by moving the lekking centre from one forest patch to another even several hundred meters between successive springs (Rolstad & Wegge 1989c, Valkeajärvi *et al.* 2007).

In spite of the positive trends between fine-grain fragmentation and lekking-area persistence, coarse-scale responses to fragmentation may also occur. In Norwegian logging experiments, clear-cuts > 20 ha promoted solitary display (Rolstad & Wegge 1989d). It is therefore possible that the pixel size used in our study (25 × 25 m) may introduce false fragmentation such that, although adjacent pixels are actually all forest, they are divided into separate classes in the data (see also Miettinen *et al.* 2005). The resulting "artificial fragmentation" may not be ecologically relevant for Capercaillie. Probably related to the nature of our landscape data, the mean forest-patch size in the surrounding areas of the leks was very small especially in northern Finland, and the mean nearest-neighbour distances were short (Table 1).

Fragmentation may also have a negative impact on the reproductive success of Capercaillie via enhanced predation pressure in fragmented landscapes (Kurki *et al.* 1997, 2000, Storaas *et al.* 1999, Storch *et al.* 2005; but see Borchtchevski *et al.* 2003). In this context, breeding females might be even more vulnerable than males. Clearly, the relationship between different measures of fragmentation and different stages of life history of Capercaillie should be further studied.

4.2. Effect of habitat loss

In Finland, Capercaillie males appear to require several types of habitat from a large area to fulfil their requirements for lekking sites. Considering the persistence of lekking areas through multiple years, the quality and amount of forests within 3,000 m (covering almost 30 km^2) from the centre of a lekking site seem to be of particular importance. This figure corroborates the Capercaillie home-range size suggested by Wegge & Rolstad (2002; 30–80 km^2). Forest cover at large spatial scales also appears to be important for the persistence of Capercaillie in Cantabria, Spain (Quevedo *et al*. 2006). If the males particularly stay in the surrounding areas of the leks almost throughout the year (Wegge & Larsen 1987), it is understandable why our result supports the estimate made by Wegge & Rolstad (2002). However, Wegge & Rolstad (2002) also pointed out that when taking into account the individuals with the largest spatial needs, a lekking population may require nearly 300 km^2. This would suggest that managers should consider more than one functioning lekking site, making the optimal "management unit" for lekking sites of Capercaillie a minimum of 400 km^2 (Wegge & Rolstad 2002), thus calling for provincial or even nation-wide planning (Lindén *et al*. 2000).

The connection between the amount of forests and the persistence of lekking areas was most pronounced in the southernmost study area. Lekking sites in Southern Finland are normally situated in larger-than-average forest patches (Lindén & Pasanen 1987, Helle *et al.* 1994, Angelstam 2004). One response to habitat loss might be that in Southern Finland, Capercaillie males may need to extend their annual home ranges and this way compensate for the increase of unsuitable habitat (Gjerde & Wegge 1989, Storch 1993, Edenius & Sjöberg 1997). In the study of Wegge & Rolstad (1986), the territory sizes of Capercaillie males were indeed larger when the surroundings of the leks contained less mature forest, and the number of adult males per lek positively correlated with the percentage of old forest surrounding the lek. The phenomenon of home-range extension has also been discovered in other woodland-dependent species, such as the Willow Tit (*Parus montanus*; Siffczyk *et al.* 2003).

Traditionally, Capercaillie has been thought to be dependent on mature or old forests (e.g., Angelstam 2004). However, the species might not be a strict specialist of old forests (e.g., Rolstad & Wegge 1987b, Helle *et al.* 1989), at least from the point of view of the persistence of lekking areas (Valkeajärvi *et al.* 2005). Our results indicate that the overall forest cover (here, forests > 60 m^3 ha^{-1}) is a good predictor for the persistence of lekking areas in Finland. In Norway, Capercaillie males have formed new lekking sites in young (26–46 years, 50–140 m^3ha^{-1}) forests (Rolstad *et al.* 2007). Moreover, in the study of Miettinen *et al.* (2005) the proportion of thinned forests (36–100 m^3 ha^{-1}) in north-eastern Finland was significantly higher around lekking sites compared to the average landscape. Apparently thinned stands and other regenerating forests are of sufficient quality for Capercaillie (Miettinen *et al.* 2005, 2008, Sirkiä *et al*. 2010).

4.3. The interaction between habitat loss and fragmentation

The observed interaction between habitat cover and fragmentation implies that as habitat cover decreases, the influence of configuration over and above that of habitat loss increases. Our results indicate that if the area of suitable habitat decreases the patch configuration may become increasingly important for the persistence of lekking areas. However, the residuals used as a measure of forest fragmentation only explain the part of fragmentation which cannot be explained by forest cover, and thus the amount of variation of fragmentation included in the measure of forest cover remains unknown.

According to Rolstad & Wegge (1987a, 1989b), if the cover of forests older than 60–70 years increases over 50%, the lekking sites will support more males per lek in these fragmented or "fine-grained" forests. Although we did not have information on the amount of males at the studied lekking sites, it is likely that a higher probability of the persistence of a lek is connected to a greater number of males at that lek (Rolstad & Wegge 1989a). Moreover, the fragmentation model of Rolstad & Wegge (1987a) predicted that the number of males per lek should increase if the mosaic grain size decreases both at high and low cover of old forests. In our model, a higher persistence of a lek was connected to fine-grain fragmentation with forests older than 40–60 years, coinciding with tree volume > 60 m^3 ha^{-1}. When the patch size becomes very small, such as in our data, the fine-grained mosaic might be experienced more or less uniform, spacious forest by Capercaillie males. This might result in another, smaller peak in the probability of lekking-area persistence. In southern and central Finland, this peak may be around 50% forest cover (for an example, see Fig. 3), reflecting the turning point in the model presented by Rolstad & Wegge (1987a). For northern Finland, the effect of the fine-grain fragmentation varied the most, and no single turning point could be detected (data not shown). Despite the insignificant interactions with study area (LOCAT), we acknowledge that there are major differences in the landscapes between the study areas, which probably partly affected the nature of fine-grain fragmentation observed in these areas.

4.4. Methodological aspects

Data on lekking sites were collected by several people, some of whom were voluntary land owners and hunters, a fact that may cause uncontrolled (but presumably random) uncertainties in the data. Moreover, the exact middle point of a lekking arena is difficult to define because it may move inside the forest area up to a few hundred meters (Rolstad & Wegge 1989c, Valkeajärvi *et al.* 2007). This fact was reflected on our choice of the examined spatial scales which should always include the exact location of the lekking arena along with the majority of the daily territories (e.g., Wegge & Larsen 1987). Overall, our data are the best available to study the persistence of Capercaillie leks in Finland, and we are confident that the general spatial and temporal patterns reported here are robust for the focal species.

There is a time lag between the observed habitat loss in the landscape and the response of the species (see Müller 1990, Ewers & Didham 2006). We tested the effect of the study period in the models and found that it was redundant concerning the effects of landscape variables. Generally this is not very surprising, because the regionally varying

legacy of the forest management history is reflected in the landscape parameters. The effect of time is therefore interlinked with changes in the landscape, in the reality of Capercaillie leks as well as in our models.

Although we decided to follow the procedure of linear regression to obtain a fragmentation index as described in Trzcinski *et al*. (1999), another, perhaps a more realistic, option would have been to fit a slightly hump-shaped regression model to the data (see Fig. 2). Landscape patterns are expected to have nonlinear relationships in reality and in artificial landscapes (e.g., Andrén 1994). Nevertheless, the trend between the PC1 and forest cover remains the same.

According to Koper *et al.* (2007), the use of residuals as an independent measure of forest fragmentation artificially leads to a stronger effect of the amount of habitat than would do a fragmentation index. Moreover, residual regression may produce biased results depending on the correlation between the amount and fragmentation of habitat, and whether the fragmentation measure has a positive or negative effect on the response variable (Smith *et al*. 2009). In addition, area effects obtained using inter-dependent measures of the amount of habitat may actually result from edge effects (Fletcher Jr. *et al.* 2007). Moreover, the apparent effect of the amount of habitat may hide within-patch and edge effects (Debuse *et al.* 2006, Koper & Schmiegelow 2006).

Acknowledging the criticism towards the residual regression technique, we performed exactly the same modelling with original values of PC1 as a fragmentation index (instead of residuals; see Smith *et al.* 2009). The interpretation of the results was essentially the same as presented above. It seems that both landscape composition and configuration are so influential to Capercaillie leks that even while using the residuals as a measure of fragmentation, we were able to detect significant habitat-loss and fragmentation effects, as well as a significant interaction between these variables. We are aware that while using residuals as an index of fragmentation we can only inspect fragmentation effects that exceed the effects incorporated in the amount of habitat. While we must caution that the effects that appear to be influenced by habitat area may include both edge effects and within-patch effects, it is biologically implausible to consider habitat area unimportant for Capercaillie leks. The size of Capercaillie lekking areas (minimum of 300 ha; Wegge & Larsen 1987) indicates that the affiliated forest area must be very large (e.g., Lindén & Pasanen 1987, Helle *et al.* 1994, Angelstam 2004).

4.5. Management guidelines, and conclusions

Forest management may positively affect species that are sensitive to habitat loss and fragmentation but are not entirely restricted to old, undisturbed forests (Huggard 2003). In this sense, the future of Capercaillie can be seen in a light of optimism, at least from the point of view of our results (see also Rolstad *et al.* 2007, Miettinen *et al.* 2008).

When considering Capercaillie conservation and management, our results support earlier guidelines given for boreal environments (Lindén & Pasanen 1987, Rolstad & Wegge 1989c, Helle *et al.* 1994, Miettinen *et al.* 2005). It is important to comprehend Capercaillie lekking sites as large units. In Finland and especially in areas suffering considerable habitat loss, the area surrounding the lekking centre within 3,000-m radius should be considered. For example, to achieve a 50% probability for the persistence of leks in southern Finland, the amount of forests older than 40 years should be close to 50% within an area with 3,000-m radius surrounding the leks, thus covering approximately 14 km^2. However, functioning leks should be considered together to guarantee the connectivity between leks. Thus, even larger spatial scales than the 14 km^2 should be covered by the managers if local lekking populations, with multiple leks, are to be conserved (Wegge & Rolstad 2002). In the case of Capercaillie management, national-level forest planning should therefore be adapted as a novel method used by the authorities (Lindén *et al.* 2000). Moreover, mosaic-like variability should be favoured (Esseen *et al.* 1997, Brotons *et al.* 2003), but not at the cost of the overall forest cover (Andrén 1994, Villard *et al.* 1999, Fahrig 2001, see also Koper *et al.* 2007). These suggestions are in line with the current forest-management guidelines in Finland (Heinonen *et al.* 2005, Metsätalouden kehittämiskeskus Tapio 2006). To conclude, the first priority seems to be to secure adequate forest cover at the large-scale

landscapes surrounding the leks (see also Miettinen *et al.* 2008), but on the lekking site itself, mosaic-like forest structure might support the growth of multi-layered forests which in turn continuously provide suitable habitat characteristics for Capercaillie. With multi-level planning and management both these aspects could be covered (see also Suchant & Braunisch 2004, Braunisch & Suchant 2007).

Acknowledgements. The study was supported by the Science Foundation of the University of Helsinki and by the Finnish Game Management Foundation. We thank Vesa Nivala for assisting in GIS analyses, and Mikko Mönkkönen and two anonymous reviewers for their valuable comments on the manuscript.

Metsän määrän ja boreaalisen metsämaiseman hienojakoisen pirstoutumisen vaikutukset metson soidinalueiden säilymiseen

Tutkimuksessa selvitettiin, ovatko metsäympäristön määrä ja pirstoutuneisuus yhteydessä metson (*Tetrao urogallus*) soidinalueiden säilymiseen kolmella tutkimusalueella Suomessa. Kaikkiaan 381 soidinpaikkaa tarkastettiin kahteen otteeseen 10–30 vuoden välein. Soidinpaikat luokiteltiin tarkastusten perusteella säilyneiksi tai hylätyiksi. Metsän määrää ja hienojakoista pirstoutumista tutkittiin satelliittihavaintoihin perustuvan metsien inventointiaineiston avulla soidinten ympärillä kahdessa eri maisemamittakaavassa (1 000 ja 3 000 m säteellä). Pirstoutumismuuttujasta poistettiin tilastollisesti metsän määrästä aiheutuva vaihtelu, ja aineisto analysoitiin logistisella regressioanalyysillä.

Tuloksien arviointiin käytettiin informaatioteoreettista mallinvalintaa. Hienojakoinen pirstoutuminen vaikutti positiivisesti soidinten säilymiseen. Metsän määrä puolestaan vaikutti positiivisesti ainoastaan silloin, kun soidinten säilymistä tarkasteltiin 3 000 m mittakaavassa. Pirstoutumisella ja metsän määrällä havaittiin negatiivinen yhteisvaikutus soidinten säilymiseen. Metsän määrän vähentyessä metsolle soveltuvien metsäkuvioiden keskinäisellä sijoittumisella voi siis olla suuri merkitys soidinalueiden säilymiselle. Tulosten mukaan tehokkaimpia metsänhoidon keinoja metson soidinalueiden säilyttämiseksi olisivat soidinpaikkojen ympäristön metsäpeitteen maksimointi ja metsien mosaiikkimaisen vaihtelevuuden suosiminen soidinalueilla.

References

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. & Soluk, D.A. 1987: Ecological neighborhoods: scaling environmental patterns. — Oikos 49: 340–346.

Andrén, H. 1994: Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. — Oikos 71: 355–366.

Angelstam, P. 2004: Habitat thresholds and effects of forest landscape change on the distribution and abundance of black grouse and capercaillie. — Ecological Bulletin 51: 173–187.

Betts, M.G., Forbes, G.J., Diamond, A.W. & Taylor, P.D. 2006: Independent effects of fragmentation on forest songbirds: an organism-based approach. — Ecological Applications 16: 1076–1089.

Borchtchevski, V.G., Hjeljord, O., Wegge, P. & Sivkov, A.V. 2003: Does fragmentation by logging reduce grouse reproductive success in boreal forests? — Wildlife Biology 9: 275–282.

Braunisch, V. & Suchant, R. 2007. A model for evaluating the 'habitat potential' of a landscape for capercaillie *Tetrao urogallus*: a tool for conservation planning. — Wildlife Biology 13 (Suppl. 1): 21–33.

Brotons, L., Mönkkönen, M., Huhta, E., Nikula, A. & Rajasärkkä, A. 2003: Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. — Landscape Ecology 18: 377–393.

Burnham, K.P. & Anderson, D.R. 1998: Model selection and inference: a practical information-theoretic approach. — Springer-Verlag, New York.

Cooper, C.B. & Walters, J.R. 2002: Independent effects of woodland loss and fragmentation in brown treecreeper distribution. — Biological Conservation 105: 1–10.

Debuse, V.J., King, J. & House, A.P.N. 2006: Effect of fragmentation, habitat loss and within-patch habitat characteristics on ant assemblages in semi-arid woodlands of eastern Australia. — Landscape Ecology 22: 731–745.

Edenius, L. & Elmberg, J. 1996: Landscape level effects of modern forestry on bird communities in North Swedish boreal forests. — Landscape Ecology 11: 325–338.

Edenius, L. & Sjöberg, K. 1997: Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. — Ecography 20: 425–431.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K.

1997: Boreal forests. — Ecological Bulletins 46: 16–47.

Ewers, R.M. & Didham, R.K. 2006: Confounding factors in the detection of species responses to habitat fragmentation. — Biological Reviews 81: 117–142.

Fahrig, L. 1997: Relative effects of habitat loss and fragmentation on population extinction. — Journal of Wildlife Management 61: 603–610.

Fahrig, L. 1998: When does fragmentation of breeding habitat affect population survival? — Ecological Modelling 105: 273–292.

Fahrig, L. 1999: Forest loss and fragmentation: which has the greater effect on persistence of forest-dwelling animals? — In Forest wildlife and fragmentation, management implications (ed. Rochelle, J.A., Lehman, L.A. & Wisniewski, J.): 87–95. Brill, Leiden.

Fahrig, L. 2001: How much habitat is enough? — Biological Conservation 100: 65–74.

Fahrig, L. 2003: Effects of habitat fragmentation on biodiversity. — Annual Review of Ecology, Evolution, and Systematics 34: 487–515.

Fletcher Jr, R.J., Ries, L., Battin, J. & Chalfoun, A.D. 2007: The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined? — Canadian Journal of Zoology 85: 1017–1030.

Forman, R.T.T. & Godron, M. 1986: Landscape ecology. — John Wiley, New York.

Fuhlendorf, S.D., Woodward, A.J.W., Leslie Jr, D.M. & Shackford, J.S. 2002: Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. — Landscape Ecology 17: 617–628.

Gjerde, I. & Wegge, P. 1989: Spacing pattern, habitat use and survival of capercaillie in a fragmented winter habitat. — Ornis Scandinavica 20: 219–225.

Graf, R.F., Bollmann, K., Suter, W. & Bugmann, H. 2005: The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. — Landscape Ecology 20: 703–717.

Haila, Y. 1990: Toward an ecological definition of an island: a northwest European perspective. — Journal of Biogeography 17: 561–568.

Hannah, L., Carr, J.L. & Lankerani, A. 1995: Human disturbance and natural habitat: a biome level analysis of a global data set. — Biodiversity and Conservation 4: 128–155.

Harrison, S. & Bruna, E. 1999: Habitat fragmentation and large-scale conservation: what do we know for sure? — Ecography 22: 225–232.

Heinonen, P., Karjalainen, H., Kaukonen, M. & Kuokkanen, P. (eds.) 2005: Metsätalouden ympäristöopas. — Metsähallitus, Edita Prima Oy.

Helle, P., Belkin, V., Bljudnik, L., Danilov, P.I. & Jakimov, A. 2003: Changes in grouse populations in Finland and Russian Karelia during the past decades. — Suomen Riista 49: 32–43. (In Finnish with English summary)

Helle, P., Helle, T. & Lindén, H. 1994: Capercaillie (*Tetrao urogallus*) lekking sites in fragmented Finnish forest landscape. — Scandinavian Journal of Forest Research 9: 386–396.

Helle, T., Helle, P., Lindén, H. & Kilpelä, S.-S. 1989: Stand characteristics of capercaillie lekking sites in northern Finland. — Suomen Riista 35: 26–35. (In Finnish with English summary)

Huggard, D.J. 2003: Use of habitat features, edges and harvest treatments by spruce grouse in subalpine forest. — Forest Ecology and Management 175: 531–544.

Isebrands, J.G. & Crow, T.R. 1975: Introduction to uses and interpretation of principal component analysis in forest biology. — USDA Forest Service, general technical report NC-17: 1–19.

Jokimäki, J., Huhta, E., Mönkkönen, M. & Nikula, A. 2000: Temporal variation of bird assemblages in moderately fragmented and less-fragmented boreal forest landscapes: A multi-scale approach. — Écoscience 7: 256–266.

Katila, M. & Tomppo, E. 2002: Stratification by ancillary data in multisource forest inventories employing k-nearest-neighbour estimation. — Canadian Journal of Forest Research 32: 1548–1561.

Keppie, D.M. & Kierstead, J.M. 2003: The need to improve our attention to scale of resolution in grouse research. — Wildlife Biology 9: 385–391.

Koper, N. & Schmiegelow, F.K.A. 2006: A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. — Landscape Ecology 21: 1045–1059.

Koper, N., Schmiegelow, F.K.A. & Merrill, E.H. 2007: Residuals cannot distinguish between ecological effects of habitat amount and fragmentation: implications for the debate. — Landscape Ecology 22: 811–820.

Kurki, S., Helle, P., Lindén, H. & Nikula, A. 1997: Breeding success of black grouse and capercaillie in relation to mammalian predator densities on two spatial scales. — Oikos 79: 301–310.

Kurki, S., Nikula, A., Helle, P. & Lindén, H. 2000: Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. — Ecology 81: 1985–1997.

Leopold, A. 1933: Game management. — Charles Scribner's Sons, New York.

Levin, S.A. 1992: The problem of pattern and scale in ecology. — Ecology 73: 1943–1967.

Lindén, H. (ed.) 2002: Metsäkanalintututkimuksia: metsäkanalintukannat. — Gummerus Kirjapaino Oy, Saarijärvi. (In Finnish)

Lindén, H., Danilov, P.I., Gromtsev, A.N., Helle, P., Ivanter, E.V. & Kurhinen, J. 2000: Large-scale forest corridors to connect the taiga fauna to Fennoscandia. — Wildlife Biology 6: 179–188.

Lindén, H., Helle, E., Helle, P. & Wikman, M. 1996: Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. — Finnish Game Research 49: 4–11.

Lindén, H. & Pasanen, J. 1987: Capercaillie leks are threatened by forest fragmentation. — Suomen Riista 34: 66–76. (In Finnish with English summary)

Lindén, H. & Rajala, P. 1981: Fluctuations and long-term trends in the relative densities of tetraonid populations in Finland, 1964-77. — Finnish Game Research 39: 13–34.

McGarigal, K. & Cushman, S.A. 2002: Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. — Ecological Applications 12: 335–345.

McGarigal, K. & Marks, B.J. 1995: FRAGSTATS – spatial pattern analysis for quantifying landscape structure. — General Technical Report PNW-GTR-351, Portland.

Metsätalouden kehittämiskeskus Tapio 2006: Hyvän metsänhoidon suositukset. — Metsäkustannus Oy, F.G. Lönnberg, Helsinki. (In Finnish)

Miettinen, J., Helle, P. & Nikula, A. 2005: Lek area characteristics of capercaillie (*Tetrao urogallus*) in eastern Finland as analysed from satellite-based forest inventory data. — Scandinavian Journal of Forest Research 20: 358–369.

Miettinen, J., Helle, P., Nikula, A. & Niemelä, P. 2008: Large-scale landscape composition and capercaillie (*Tetrao urogallus*) density in Finland. — Annales Zoologici Fennici 45: 161–173.

Müller, F. 1990: Habitat linking – a means of saving remnant grouse population in Central Europe. — In Proceedings of the 4th International Grouse Symposium. September 1987, Lam, West Germany.

Mönkkönen, M. 1999: Managing Nordic boreal forest landscapes for biodiversity: ecological and economic perspectives. — Biodiversity and Conservation 8: 85–99.

Niemuth, N.D. & Boyce, M.S. 2004: Influence of landscape composition on sharp-tailed grouse lek location and attendance in Wisconsin pine barrens. — Écoscience 11: 209–217.

Norton, M.R., Hannon, S.J. & Schmiegelow, F.K.A. 2000: Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. — Ecography 23: 209–223.

Pakkala, T., Pellikka, J. & Lindén, H. 2003: Capercaillie (*Tetrao urogallus*) – a good candidate for an umbrella species in taiga forests. — Wildlife Biology 9: 309–316.

Peltola, A. 2003: Forest Resources. — In Finnish Statistical Yearbook of Forestry 2003 (ed. Peltola, A.): 31–69. Finnish Forest Research Institute, Helsinki.

Quevedo, M., Bañuelos, M.J. & Obeso, J.R. 2006: The decline of Cantabrian capercaillie: How much does habitat configuration matter? — Biological Coservation 127: 190–200.

Raivio, S. & Haila, Y. 1990: Bird assemblages in silvicultural habitat mosaics in southern Finland during the breeding season. — Ornis Fennica 67: 73–83.

Rolstad, J., Rolstad, E. & Wegge, P. 2007: Capercaillie *Tetrao urogallus* lek formation in young forest. — Wildlife Biology 13 (Suppl. 1): 59–67.

Rolstad, J. & Wegge, P. 1987a: Distribution and size of capercaillie leks in relation to old forest fragmentation. — Oecologia 72: 389–394.

Rolstad, J. & Wegge, P. 1987b: Habitat characteristics of Capercaillie Tetrao urogallus display grounds in southeastern Norway. — Holarctic Ecology 10: 219–229.

Rolstad, J. & Wegge, P. 1989a: Effects of logging on capercaillie *Tetrao urogallus* leks. III. Extinction and recolonization on lek populations in relation to clearfelling and fragmentation of old forest. — Scandinavian Journal of Forest Research 4: 129–135.

Rolstad, J. & Wegge, P. 1989b: Capercaillie *Tetrao urogallus* populations and modern forestry – a case for landscape ecological studies. — Finnish Game Research 46: 43–52.

Rolstad, J. & Wegge, P. 1989c: Effects of logging on capercaillie *Tetrao urogallus* leks. I. Cutting experiments in Southcentral Norway. — Scandinavian Journal of Forest Research 4: 99–109.

Rolstad, J. & Wegge, P. 1989d: Effects of logging on capercaillie *Tetrao urogallus* leks. II. Cutting experiments in Southeastern Norway. — Scandinavian Journal of Forest Research 4: 111–127.

Sachot, S., Perrin, N. & Neet, C. 2003: Winter habitat selection by two sympatric forest grouse in western Switzerland: implications for conservation. — Biological Conservation 112: 373–382.

Schmiegelow, F.K.A. & Mönkkönen, M. 2002: Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. — Ecological Applications 12: 375–389.

Siffczyk, C., Brotons, L., Kangas, K. & Orell, M. 2003: Home range size of willow tits: a response to winter habitat loss. — Oecologia 136: 635–642.

Sirkiä, S., Lindén, A., Helle, P., Nikula, A., Knape, J. & Lindén, H. 2010: Are the declining trends in forest grouse populations due to changes in the forest age structure? A case study of capercaillie in Finland. — Biological Conservation 143: 1540–1548.

Sjöberg, K. 1996: Modern forestry and the capercaillie. — In Conservation of Faunal Diversity in Forested Landscapes (ed. DeGraaf, R.M. & Miller, R.I.): 111–135. Chapman & Hall, London.

Smith, A.C., Koper, N., Francis, C.M. & Fahrig, L. 2009: Confronting collinearity: comparing methods for disentangling the effects of habitat loss and fragmentation. — Landscape Ecology 24: 1271–1285.

Storaas, T., Kastdalen, L. & Wegge, P. 1999: Detection of forest grouse by mammalian predators: a possible explanation for high brood losses in fragmented landscapes. — Wildlife Biology 5: 187–192.

Storch, I. 1993: Patterns and strategies of winter habitat selection in alpine capercaillie. — Ecography 16: 351–359.

Storch, I. 1997: Male territoriality, female range use, and

spatial organisation of capercaillie *Tetrao urogallus* leks. — Wildlife Biology 3: 149–161.
Storch, I. 2000: Conservation status and threats to grouse worldwide: an overview. — Wildlife Biology 6: 195–204.
Storch, I. 2002: On spatial resolution in habitat models: can small-scale forest structure explain capercaillie numbers? — Conservation Ecology 6: 6. http://www.consecol.org/vol6/iss1/art6/
Storch, I. 2007: Conservation status of grouse worldwide: an update. — Wildlife Biology 13 (Suppl. 1): 5–12.
Storch, I., Woitke, E. & Krieger, S. 2005: Landscape-scale edge effect in predation risk in forest-farmland mosaics of central Europe. — Landscape Ecology 20: 927–940.
Suchant, R. & Braunisch, V. 2004: Multidimensional habitat modeling in forest management – a case study using capercaillie in the Black Forest, Germany. — Ecological Bulletins 51: 455–469.
Thiel, D., Unger, C., Kéry, M. & Jenni, L. 2007: Selection of night roosts in winter by capercaillie *Tetrao urogallus* in Central Europe. — Wildlife Biology 13 (Suppl. 1): 73–86.
Tokola, T. & Heikkilä, J. 1997: Improving satellite image based forest inventory by using a priori site quality information. — Silva Fennica 31: 67–78.
Tomppo, E., Olsson, H., Ståhl, G., Nilsson, M., Hagner, O. & Katila, M. 2008: Combining national forest inventory field plots and remote sensing data for forest databases. — Remote Sensing of Environment 112: 1982–1999.
Trzcinski, M.K., Fahrig, L. & Merriam, G. 1999: Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. — Ecological Applications 9: 586–593.
Valkeajärvi, P. & Ijäs, L. 1986: On the display requirements of capercaillie in Central Finland. — Suomen Riista 33: 5–18. (In Finnish with English summary)
Valkeajärvi, P., Ijäs, L. & Lamberg, T. 2005: Metson soidinpaikat siirtyvät. — Metsästäjä 54: 22–25. (In Finnish)
Valkeajärvi, P., Ijäs, L. & Lamberg, T. 2007: Capercaillie display grounds move – short and long term observations. — Suomen Riista 53: 104–120. (In Finnish with English summary)
Villard, M.-A., Trzcinski, M.K. & Merriam, G. 1999: Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. — Conservation Biology 13: 774–783.
Wegge, P., Kvålsgard, T., Hjeljord, O. & Sivkov, A.V. 2003: Spring spacing behaviour of capercaillie Tetrao urogallus males does not limit numbers at leks. — Wildlife Biology 9: 283–289.
Wegge, P. & Larsen, B.B. 1987: Spacing of adult and subadult male common capercaillie during the breeding season. — Auk 104: 481–490.
Wegge, P. & Rolstad, J. 1986: Size and spacing of capercaillie leks in relation to social behavior and habitat. — Behavioral Ecology and Sociobiology 19: 401–408.
Wegge, P. & Rolstad, J. 2002: Storfuglen og skogbruket: et sammandrag fra 20 års undersøkelser I Varald statskog, Hedmark. — In Seminarrapport IBN-SEVU, Norges Landbrukshøyskole, Ås. (In Norwegian)
Wiens, J.A. 1989: Spatial scaling in ecology. — Functional Ecology 3: 385–397.
Winqvist, T. 1983: 100 tjäderplatser. — Sveriges Skogsvårdsförbunds Tidsskrift 2: 4–25. (In Swedish)
With, K.A. & Crist, T.O. 1995: Critical thresholds in species' responses to landscape structure. — Ecology 76: 2446–2459.